ON THE DENTITION AND TOOTH REPLACEMENT IN TWO BAURIAMORPH REPTILES

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(With 3 plates and 10 figures in the text)

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Introduction

The bauriamorphs are an advanced group of mammal-like reptiles which have independently developed many mammalian features otherwise found only in the cynodonts and mammals. Broom (1911) suggested that because of their less specialized nature the bauriamorphs are probably more closely allied to the group from which mammals arose than the cynodonts are. He suggested (1932) that the ictidosaurs (including *Diarthrognathus*) probably arose from a small bauriamorph that lived during *Cynognathus* zone times. The structure of the skull of *Diarthrognathus* (Crompton, 1958) confirms this view.

Very little detailed information on the dentition of bauriamorphs is available and the purpose of the present paper is to record information on the dentitions of two, *Ericiolacerta* and *Bauria*.

Recently a detailed study of the dentition of *Diarthrognathus* has been completed by the author; this will be published in the near future. The present study will therefore enable the possible relationships of this advanced mammal-like reptile to be discussed with greater confidence.

Information reported here on *Ericiolacerta parva* is based on the type and only known specimen of this animal and is in addition to that published by Watson (1931) in his excellent description of this animal. As many teeth as possible were exposed and the left mandible was separated from the skull.

The present description of the dentition of *Bauria cynops* is based upon the type skull (S.A.M. 1333) described by Broom (1909). The exposed surface of the skull had been damaged but fortunately little attempt was made to prepare

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individual teeth and consequently much useful information could still be obtained. In order that the teeth could be studied in detail the lower jaw was freed from the skull. Unfortunately the matrix does not respond to acetic acid and it was therefore necessary to prepare the teeth mechanically.

Short descriptions of the dentition of *Bauria* have been given by Broom (1909, 1932, 1937), Boonstra (1938) and Brink (1953); these are based upon three skulls and an isolated mandible. Considerable diversity of opinion exists on several important aspects of the dentition. Little detailed information is available on the dentitions of the other bauriamorphs *Bauroides*, *Melinodon*, *Sesamodon* and *Watsoniella*. Seeley (1895) has given a description of the post-canines of *Microgomphodon* and *Microhelodon*. Unfortunately it is difficult to follow, and no illustrations accompany the description.

The importance of *Ericiolacerta* is that it is the earliest theriodont that is known in which the apices of the crowns of marginal teeth occlude and were worn to horizontal or spherical surfaces. In the scaloposaurids and early cynodonts the postcanines are longitudinally ovate and sheared past one another to achieve a scissor-like cutting action. In the *Cynognathus* zone bauriamorphs, the gomphodont cynodonts, and their descendants the tritylodontids, the cheek teeth are transversely widened and occluding crowns met one another. *Ericiolacerta* is therefore an ideal animal to study the shift from a shearing to a crushing or grinding tooth action. A similar shift took place in the early mammals (Patterson, 1956), and an attempt will be made in this paper to compare the jaw action of early mammals with those of some mammal-like reptiles in order to determine whether or not grinding was achieved in the theriodonts with transversely ovate postcanine teeth.

Tooth replacement in the mammal-like reptiles and the origin of the mammalian type of tooth replacement has not received a great deal of attention. Watson (1931) described as unique among mammal-like reptiles the replacement of a maxillary tooth in *Ericiolacerta* vertically from above. He concluded from this study that all the functional teeth belonged to one set and that the replacing tooth observed indicated that tooth change affecting all the teeth was about to set in and that it probably only occurred once. This would mean that in *Ericiolacerta* a mammalian type of replacement had almost been achieved. Boonstra (1938) showed that in both the maxilla and dentary of *Bauria* replacing teeth lay lingual to the functional postcanines, but unfortunately he gave no detailed description. Parrington (1936) showed that in *Dimetrodon*, *Thrinaxodon* and *Tribolodon* replacement was alternate and that it was possible to divide the postcanine teeth into two series that are situated alternately in the jaw. He expressed the view that the number of replacements of each series was reduced in *Thrinaxodon*. He accepted as possible Bolk's theory for the origin of the mammalian type of replacement, viz. that as the teeth crowns became more complex there was no space for teeth of one series to erupt between those of the other and that instead one series replaced the other to form the deciduous and permanent dentitions of mammals.

Romer and Price (1940) confirmed that replacement was alternate in *Dimetrodon*, but that in addition a wave of replacement passed along each alternately numbered series. These waves passed from back to front.

Tooth replacement in gomphodont cynodonts has been described and discussed by Broom (1913), Brink (1955, 1956) and Crompton (1955b, 1958). It is at present also being studied by Mr. S. Fourie. Brink is of the opinion that although forms such as *Diademodon* from the Lower Trias do not have a dental succession identical to that of placental mammals, the incisors and anterior four postcanines were replaced only once, the 12th to 16th teeth never, and the 5th to 11th certainly not more than once. The canine, Brink feels, was probably replaced more than once. This would suggest that gomphodont cynodonts were tending towards a mammalian dental succession. Unfortunately Brink has not described the material upon which these conclusions are based.

Gomphodont cynodonts from the Middle Trias, such as *Scalenodon*, do not confirm this view (Crompton, 1955b, 1958). Here there appears to have been frequent replacement of the incisors and canines, whereas in the postcanine series replacement is limited and is recorded only from the posterior end of the dentition where sectorial teeth were replaced by transversely ovate teeth. With growth, teeth are added to the postcanine row posteriorly, while teeth are lost at the front of the postcanine row. Recent unpublished work on *Diademodon* by Mr. Fourie confirms that postcanine teeth are lost anteriorly and added posteriorly. Similar observations have been made on *Oligokyphus* (Kühne, 1956). The dental succession of gomphodont cynodonts therefore appears to be fundamentally different from that of placental mammals, and the origin of the mammalian pattern must be searched for in other mammal-like reptile groups.

Kermack (1956) has reported on tooth replacement in the Therocephalia and the Gorgonopsia. He claims that alternate replacement (his 'functional distichical replacement') has been lost in the postcanine series in these families. His material was insufficient to enable him to determine the order of replacement except in the case of the canines.

Recently Edmund (1960) has surveyed in great detail tooth replacement in the lower vertebrates. Although mammal-like reptiles are not treated above the pelycosaur level, Edmund's contribution is a most valuable basis for the study of tooth replacement in mammal-like reptiles. In order to explain mammalian tooth replacement, which is so different from the alternating replacement typical of most reptiles, Edmund has suggested that the deciduous and permanent dentitions represent individual *zahnreihen.*

It is hoped that a description given in this paper of the conditions in *Ericiolacerta* and *Bauria* will contribute towards the solution of the problem of the origin of the mammalian dental succession.

I am deeply indebted to Professor D. M. S. Watson for his very kind permission to undertake additional preparation on the type of *Ericiolacerta parva*, and to Dr. K. A. Kermack and Mrs. F. Mussett for their valuable assistance to me during my stay in London. I wish also to record my thanks to Dr. F. R. Parrington for his helpful criticism and encouragement.

Dentition and Tooth Replacement in *Ericiolacerta*

It is difficult to determine the number of teeth present in the type because the tip of the snout is slightly damaged. Watson (1931) claimed 6 teeth in the premaxilla and 8 in the maxilla and that no canine could be distinguished. Although a total of 14 teeth is probably correct it is difficult to be certain of the exact number in the maxilla and premaxilla.

Cheek teeth in both mandible and maxilla are preserved in various stages of the replacement cycle. These can be conveniently divided into four stages (fig. 1). In stage I a freshly erupted tooth was loosely held in an enlarged

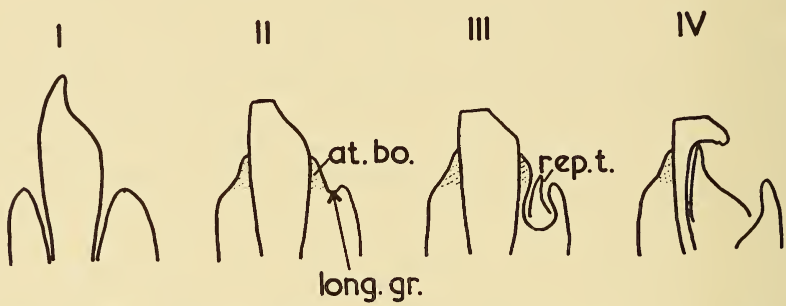

Fig. 1.—*Ericiolacerta parva*. Four stages in the replacement cycle of cheek teeth. (Key to lettering, p. 255.)

alveolus. In a later stage (II) attachment bone (at. bo.) was built up around the neck of the tooth above the longitudinal groove (long. gr.) which extended the length of the tooth row on the lingual side in the maxilla and dentary. Next, replacement teeth developed in pits in the base of the longitudinal groove (stage III), and as the replacing tooth increased in size, it migrated labially and resorbed first the alveolar wall separating it from the alveolus and second the root of the functional tooth (stage IV).

For description purposes the teeth are numbered consecutively from the front because no distinct canine is present.

Lower dentition (figs. 2 A, B, 4 C)

The 15th tooth from the front has a well-preserved unworn tricuspid crown. The central cusp is slightly higher than the accessory cusps. The outer surface of the tooth is convex, but due to a slight swelling on the inner surface of the crown a short distance below the apex of the main cusp the upper portion of the inner surface of the upper half of the crown is slightly concave (figs. 2 B, 14). The posterior lower teeth of *Ericiolacerta* behind the 8th all have this characteristic shape. The tooth is firmly held and the longitudinal groove does not extend as far posteriorly as this point. The 14th tooth is less firmly held.

The crown is unworn and in contrast to the 15th is terminated by four small cusps. The second cusp from the anterior border is the largest. Their apices do not lie in the same plane but are arranged to form an arc. A wide gap separates the 12th and 14th teeth. The functional tooth appears to have been lost, although this could not be confirmed beyond doubt. A pit in the base of the longitudinal groove containing a replacing tooth (fig. 2 A, rep. t. 13) is

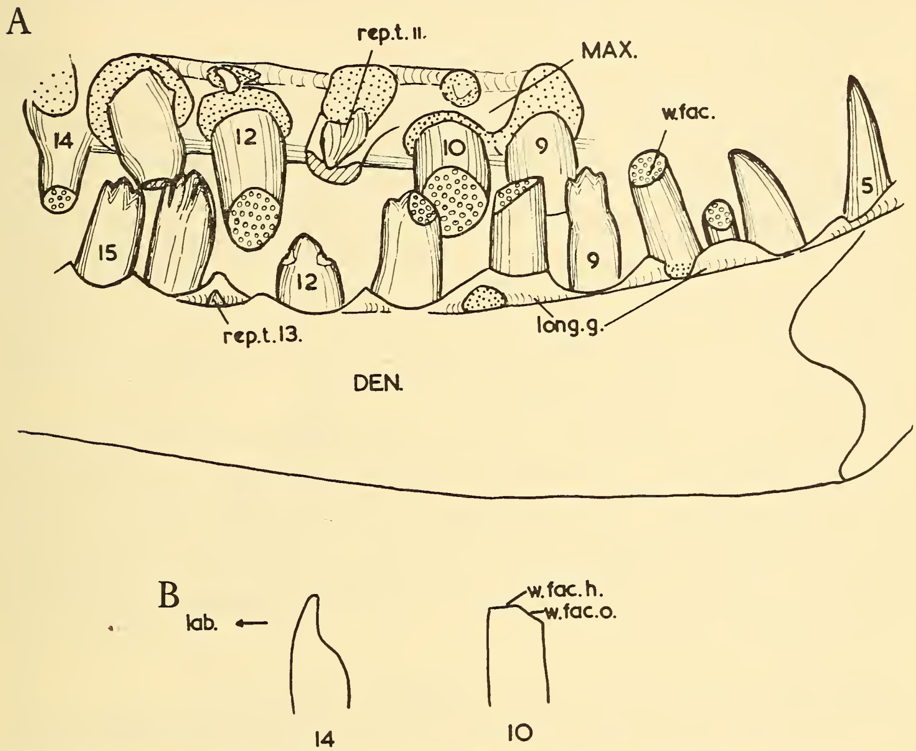

FIG. 2.—*Ericiolacerta parva*. A, medial view of posterior portion of the left upper and lower dentitions, and B, posterior view of 14th and 10th teeth. Both × 10. (Key to lettering, p. 225.)

present lingual to this gap. It has been interpreted as a replacing tooth for the 13th.

The 12th tooth is partially erupted (stage I). The accessory cusps have been lost as a result of damage but there is no sign of wear on the remaining central cusp. The 11th is fairly tightly held (stage II) and the longitudinal groove is present lingual to its base. An oblique wear facet sloping inwards and downwards has obliterated all trace of the anterior accessory cusps. The 10th is tightly held and a large pit is present lingual to it in the base of the longitudinal groove (stage III). The matrix was not completely removed from this pit and it presumably contained a replacing tooth in life. The crown is considerably worn and two distinct facets can be identified (fig. 2 B 10): a horizontal facet (w. fac. h.) on the labial side, and an oblique facet (w. fac. o.) on the lingual. The portion of the crown supporting cusps was completely worn away. The 9th tooth is loosely held by its alveolus (stage I). It shows no signs of wear and is terminated by three small cusps. The upper portion of the crown is slightly narrower antero-posteriorly than the lower, and the tooth therefore has a dumb-bell appearance. The 8th tooth is tightly held. A small pit is present in the longitudinal groove lingual to its base (stage III). The crown is worn to two distinct facets, as is the 10th.

It is difficult to interpret the 7th tooth. It is very small; the crown is extensively worn and tightly held by attachment bone. The crown surface is considerably lower than adjacent teeth. No pit is visible at the base of the longitudinal groove. The 7th tooth in the upper jaw is also small and has been considered by Watson (1931) as the first maxillary tooth. No. 6 in the lower jaw is loosely held by its alveolus, indicating that fossilization took place soon after it had erupted (stage I). It is sharply differentiated from the unworn teeth in the posterior portion of the jaw in that the crown is terminated by a single sharp cusp. In view of this it is possible to interpret it as a canine and the 7th as the first postcanine. The crown of the 5th tooth also consists of a single cusp, but it is more tightly held by attachment bone than the 6th. A fairly wide gap separates the 5th and 6th teeth.

The anterior mandibular teeth are only well preserved on the right, where six alveoli, some with and some without teeth, could be counted. The 6th tooth is well worn. The 5th is unworn and, in contrast to conditions on the left, is terminated by 3 cusps as in the left 9th and 15th teeth. The crown of the 4th tooth is extensively worn to two wear facets as in the left 10th. The 3rd alveolus is empty, the 2nd tooth is not well preserved, and the 1st appears to be a replacing tooth.

Upper dentition (Plate XII A; figs. 2 A, 3 A, B, C, 4 A, B)

The teeth of the maxillae are shown in lateral view in Plate XII A, medial view in figs. 2 A and 3 A, and in crown view in fig. 3 B. They vary greatly in size, and as in the lower jaw large spaces separate the individual teeth.

The maxilla medial and posterior to the 14th tooth is damaged, but it appears that this tooth was tightly held and that a large pit (fig. 3 B p.) was present lingual to it (stage III). A single flat wear-facet dipping slightly upwards in a lingual direction is present. The 13th is preserved as it was after it erupted and is loosely held in a large alveolus that extends lingually to the longitudinal groove (stage I). The apex of the crown has unfortunately been damaged and lost, but no signs of wear could be detected on the remaining portion. The crown of the 12th tooth is well worn to a single facet (fig. 3 C 12). The tip of the crown of a replacing tooth is present in a pit lingual to its base (stage III). The 11th tooth and its replacing tooth have been described by Watson (1931). This is the only position where stage IV of the replacement cycle is preserved, viz. in which a replacement tooth is preserved shortly before it was to have erupted. The lingual portion of root of the functional tooth (rem. f. 11) has been resorbed and the crown lost. The crown of the replacing tooth (rep. t. 11) fits closely against the remnant of the root of the functional tooth. The pit containing the replacing tooth is extremely large and confluent with the alveolus. The crown of the replacing tooth is terminated by a single cusp. The tooth as seen in posterior view is illustrated in figure 3 C, 11. A small replacing tooth (rep. t. 10) is present medial to the 10th tooth (stage III). The crown

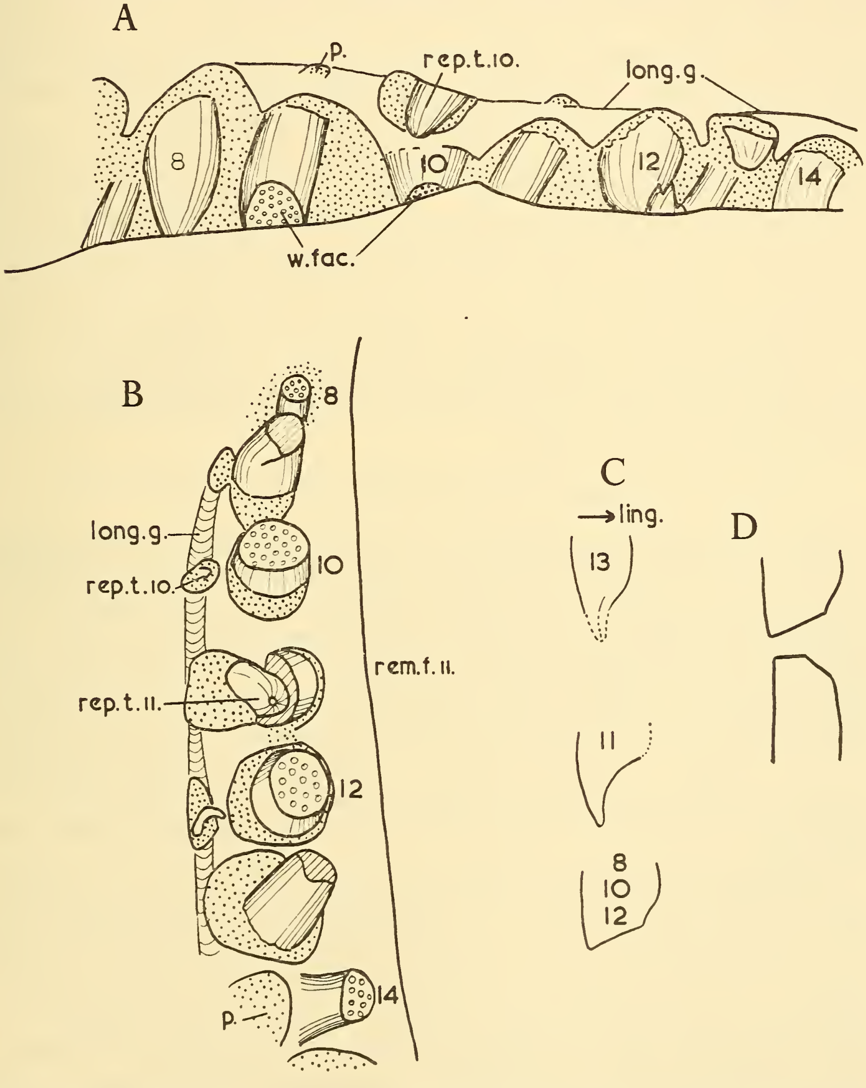

FIG. 3.—*Ericiolacerta parva.* A, medial view of upper right dentition; B, crown view of upper left dentition; C, posterior view of 13th, 11th and 8th, 10th, 12th teeth and D, occlusion of upper and lower teeth. All × 10. (Key to lettering, p. 255.)

is extensively worn to a nearly horizontal wear-facet (fig. 3 C 10). The 9th tooth is preserved as it was shortly after it erupted. The apex of the crown has been damaged but no signs of wear could be detected on the remaining portion. The 8th tooth is much smaller than the 9th, is tightly held and extensively worn, but the matrix medial to it and the three anterior teeth could not be removed without difficulty to determine details of replacement. The 7th tooth (Watson's first maxillary tooth) is smaller than the 8th and has a slightly worn crown. It is separated by a large gap from the 8th. It could not be ascertained whether a tooth has been lost from this gap. No. 6 is sharply pointed and shows no signs of wear whereas the apex of No. 5 is worn to a horizontal facet (Plate XII). No. 6 could possibly be interpreted as a small canine, and this would confirm the findings in the lower jaws.

The crowns of the teeth in the right maxilla (fig. 3 A) could only be seen in lingual view because the right cheek is covered by an articulated hand. Nos. 14, 12 and 8 are preserved as they were shortly after they erupted and no signs of wear could be detected in these teeth (stage I). The 9th and 11th teeth have small pits for replacing teeth at their bases, and the crown of the 9th is worn to an oblique wear-facet. The 13th is preserved with the crown of a well-developed replacing tooth situated in a pit medial to it (stage III). The 10th is very tightly held by attachment bone and has a well-worn crown. The replacement tooth lingual to it is the largest in the right maxilla and at death was presumably about to erupt.

Tooth replacement and tooth wear in ERICIOLACERTA

The teeth are preserved in different stages of replacement, and it is clear that the functional teeth do not belong to one series all of which were about to be replaced by a second set, as suggested by Watson (1931). It is also clear from the above description that replacing teeth developed initially in shallow pits at the base of the longitudinal groove, i.e. lingual to the functional teeth. The longitudinal groove probably supported the dental lamina. As the tooth germs increased in size, a pit developed at the base of the groove to support them. As the tooth enlarged it migrated labially, absorbing first the lingual alveolar wall and later the root of the functional tooth. Only in its final stages was replacement vertically from above or below in the upper and lower jaw respectively.

It remains now to determine the order of replacement. In fig. 4 the various stages of replacement in the left and right maxillae and the left mandible are shown diagrammatically. In the maxilla the order of replacement was clearly alternate. In the left maxilla the odd-numbered teeth, 9 and 13, have unworn crowns and are preserved as they were shortly after they erupted. Replacement of the 11th lagged slightly behind the other odd-numbered teeth, but its replacement tooth is large and in life would have been the next tooth to erupt. On the other hand the even-numbered teeth 14, 12, 10 and 8 all have worn crowns, are firmly held by their alveoli, and have small pits for replacing teeth lingual to them. In the right maxilla the even-numbered series consisting of the 8th, 12th and 14th teeth are preserved recently after they erupted. Eruption of the 10th replacement tooth would have lagged slightly behind these teeth as in the case of the 11th in the left maxilla. It therefore appears that on the left the odd teeth were erupting whereas on the right the even teeth were erupting. This may indicate that the teeth have been incorrectly numbered, but not necessarily because a similar phenomenon was encountered by the author in early cynodonts. A small difference in the degree of development of the

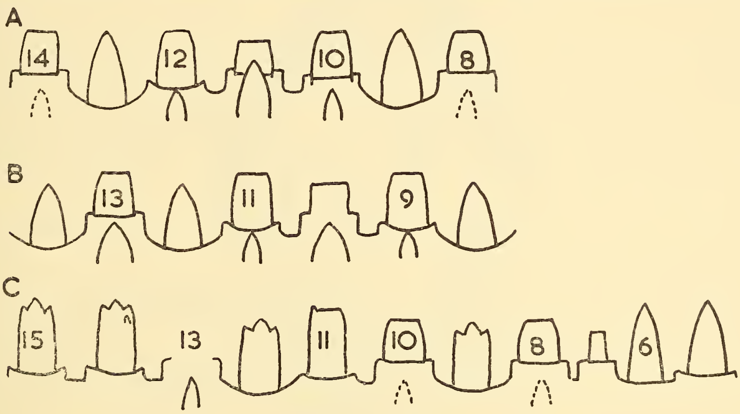

Fig. 4.—*Ericiolacerta parva.* Diagrammatic representation of the order of replacement of the posterior teeth. A, left maxilla; B, right maxilla and C, left dentary.

replacing teeth is also preserved in the odd-numbered series. The replacing tooth for the 13th is larger than those for the 9th and 11th.

Except for these minor differences it appears that alternate teeth developed and erupted simultaneously. Similar results were obtained in *Thrinaxodon* (Parrington, 1936). This is in contrast to early *Cistecephalus* zone cynodonts (Crompton, unpublished MS.) and other early therapsids (Romer and Price, 1940), where a wave of replacement passes from back to front along each alternately numbered series.

It is difficult to interpret the order of replacement in the mandible. Replacement does not appear to be of the regular alternate type observed in the maxilla. Over certain short distances there is evidence of alternate replacement, e.g. 10 and 8, while over others there is not. Unfortunately, the right lower dentition could not be studied.

Wear of the teeth

The wear surfaces indicate that the upper and lower teeth must have occluded crown to crown, and opposing upper and lower teeth did not shear past one another. Teeth preserved recently after they erupted show no signs of wear whereas teeth about to be replaced appear to have lost approximately half of their crowns as a result of wear.

It is difficult to interpret the wear-facets of occluding teeth. Upper teeth have a single flat wear-facet sloping upwards and inwards, whereas lower teeth have two distinct facets, a labial horizontal facet and a flat inner facet sloping inwards and downwards. Sharp angles are formed where the facets meet the edges of the crowns and one another (fig. 3 D). It is difficult to determine the jaw actions causing these wear-facets. It is unlikely that a single dorso-ventral

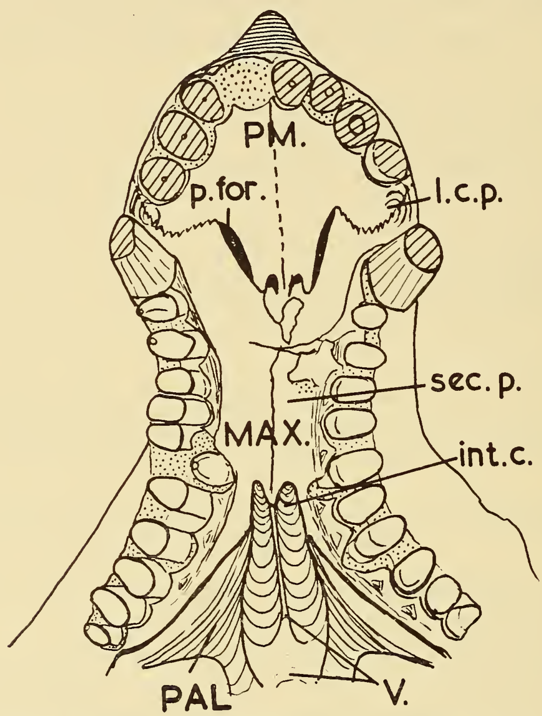

FIG. 5.—*Bauria cynops*. Ventral view of palate × 1½. (Key to lettering, p. 255.)

movement of the lower jaw would account for their shape. It is also unlikely that the abrasive action of food particles would produce such constant and sharply defined wear-facets. It is possible, therefore, that in *Ericiolacerta* more complex jaw movements were possible.

Watson (1931) has described upper cheek teeth as '. . . transversely widened, the high original cusp passing on its lingual side into a ridge which separates two concave areas into which grind the posterior and anterior cusps of the two lower molars between which it fits'. The present study does not confirm this arrangement. The wear patterns clearly show that the labial cusps of the uppers did not occlude outside the opposing lowers. On the contrary, the apices of the crowns when present must have met one another. The teeth are not transversely expanded to the extent suggested by Watson, and at their bases the crowns are circular in cross-section.

The Dentition of *Bauria cynops*

The palate (Plate XIII A and fig. 5) has been well described by Boonstra (1938) and Broom (1937). The secondary palate (sec. p.) is formed only by the premaxillae and maxillae. It is narrowest across the posterior border which lies adjacent to the 5th postcanines. Anteriorly to the posterior border of the secondary palate the maxillae curve sharply upwards to their contact with the premaxillae (P.M.). The premaxillae have a broad tongue-shaped process which extends backwards in the mid-line to meet the maxillae. Two ovoid foramina (p. for.) are present between the lateral edges of this structure and the maxillae. These foramina were not reported by Boonstra or Broom. From the anterior edge of these foramina an interdigitated suture between the premaxillae and maxillae passes outwards through the diastema between the last incisor and the canine. No evidence for Broom's view that part of the vomer is visible between the premaxillae and maxillae could be found.

Upper dentition (Plates XII B, XIII, and figs, 5, 6, 8)

There are 4 incisors, 1 canine and 10 postcanines in the upper jaw. This is in agreement with the findings of Broom (1909), Boonstra (1938) and Brink and Kitching (1953). The roof of the diastema between the incisors and canines has the form of a shallow pit and receives the lower canine. A thin strip of the maxilla forms a labial border to this pit and therefore the tip of the lower canine was not visible when the jaws were closed. The crowns of all the incisors and both canines were damaged, but the postcanines are fairly well preserved, except for damage to their outer surfaces. Because of this damage it was essential to prepare both left and right dentitions. The postcanines of each side are arranged to form a curve. In the region of the 5th postcanines the opposing curves are closest to one another, and anterior and posterior to this point they diverge away from each other (fig. 5). Figures of the length of the postcanine series are of little value unless it is clearly stated how the measurements were taken. Measured along the lingual surface of the upper postcanine series they measure 4·1 cm.

In crown view (fig. 6) the postcanines are oval with the lingual side of the crown considerably wider than the labial. Brink and Kitching (1953) claimed that in the third specimen of *Bauria* the crowns of adjacent teeth expand so that they come into contact with one another, but that their necks are separated from one another. It is clear in the type, however, that the majority of the postcanines were separated by narrow gaps with an average width of 0·6 mm., although in some cases teeth have been slightly displaced with the result that consecutive crowns touch one another.

The form of the crowns of the teeth is of great interest because of the marked changes they undergo as a result of wear. These changes are essential for the interpretation of jaw action and tooth replacement, and will therefore be described in detail. Interpretation of the wear pattern is complicated by

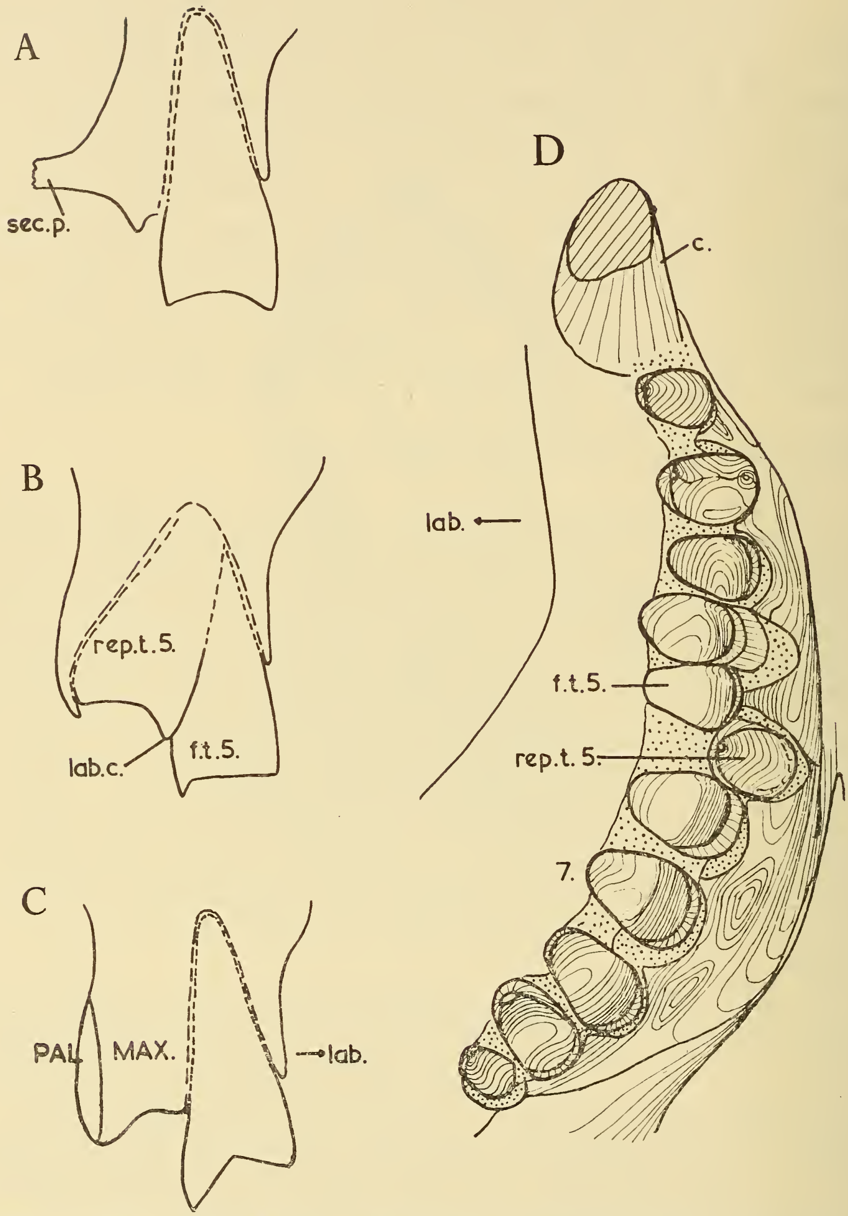

Fig. 6.—*Bauria cynops*. A, B and C, reconstructed sections through the 4th, 5th and 7th right upper postcanines and D, crown view of the upper postcanine dentition. All × 3. (Key to lettering, p. 255.)

the fact that the occluding tooth rows do not lie parallel to one another, but at a small angle to one another. The majority of the upper postcanines lie slightly further lingually to the lowers, but the anterior upper postcanines and canines lie slightly labially of the corresponding lower teeth.

In order to understand the shape of the crowns, outline drawings of the posterior view have been given in addition to the crown views (fig. 8). The 5th postcanine (fig. 6 B, rep. t. 5) on the right side was preserved shortly before it was due to be replaced, and both the replacing and functional teeth are in good condition (Plate XII B). Contrary to all previously published reports, the crown of an unworn upper tooth is not flat. On the contrary, it supports a prominent cusp (lab. c.) on the narrow labial edge of the crown while the wide lingual edge of the crown supports a crenulate ridge. In posterior view the crown has a concave centre, the centre point of the concavity lying towards the labial side of the crown. A broad, ill-defined transverse ridge extends a short distance across the crown from the apex of the main cusp. On either side the crown falls slightly away. On the left side the replacing tooth of the 5th postcanine was preserved shortly after it had fully erupted and become the functional tooth; it has the same crown structure as the incompletely erupted counterpart on the right.

The 9th, 7th and 4th are little worn, and a labial cusp and prominent lingual edge can still be recognized. The 2nd upper postcanine is also little worn and consists of a high labial cusp and small, ill-defined lingual ridge at a much higher level than the labial cusp. Wear is greater on the lingual side in this tooth, whereas in the posterior teeth wear is greatest on the labial side. This is due to the crossing of upper and lower postcanine rows. In the 8th and 6th the crowns show advanced stages of wear. Two prominent wear-facets are visible. The labial cusp has been worn away completely to a flat wear-facet extending lingually and slightly upwards to the centre of the crown where it meets a flat oblique wear-facet extending upwards and inwards from the lingual edge of the crown. The orientation of these wear-facets is best seen in the posterior profiles and stereo-photographs.

In the functional 5th postcanine on the right, wear had proceeded further. The labial wear-facet extends further across the crown. The prominent lingual edge and oblique lingual wear-facet have been considerably reduced in size. In the 3rd tooth the crown is worn to a practically horizontal plane. The 1st and 10th postcanines are considerably smaller than the other postcanines and consist of a high labial cusp lingually of which the crown falls away rapidly. The measurements of the individual postcanines in mm. are as follows:

	1	2	3	4	5	6	7	8	9	10
Max. ant.-post.	2·2	2·4	2·5	2·8	3·0	2·9	3·1	2·7	2·7	2
Max. ling.-lab.	3·8	3·9	4·1	4·7	5·3	4·7	5·1	4·3	2·9	2

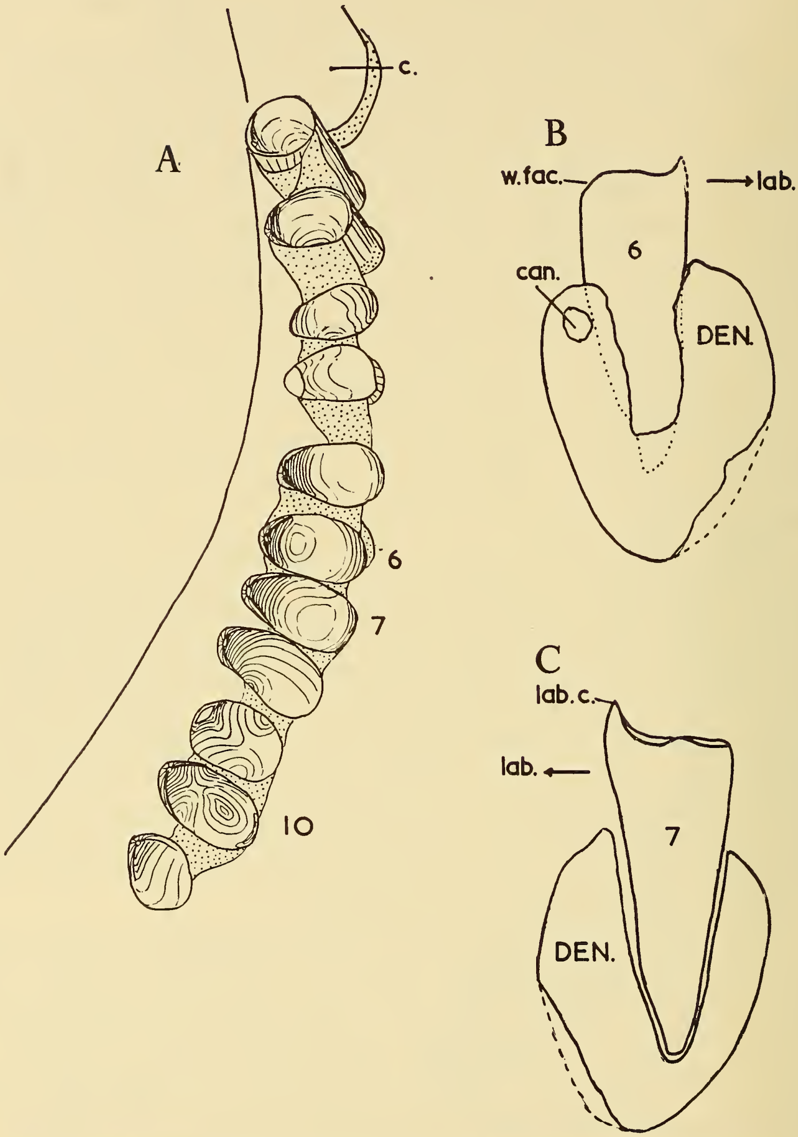

FIG. 7.—*Bauria cynops*. A, crown view of lower postcanines and B and C, sections through mandible to show the roots of the 6th and 7th postcanines. All × 3. (Key to lettering, p. 255.)

Lower dentition (Plate XIV; figs. 7, 8, 9)

There are three lower incisors. This confirms the findings of Brink and Kitching (1953). It is easy to understand why Broom (1909) considered that the type had four. A narrow diastema separates the 3rd lower incisor from the canine. The crown of the 4th upper canine fits into this diastema. The anterior region of the snout is damaged in the type in such a way that the crown of the upper 4th incisor is preserved fitting into this diastema, and is broken off at the

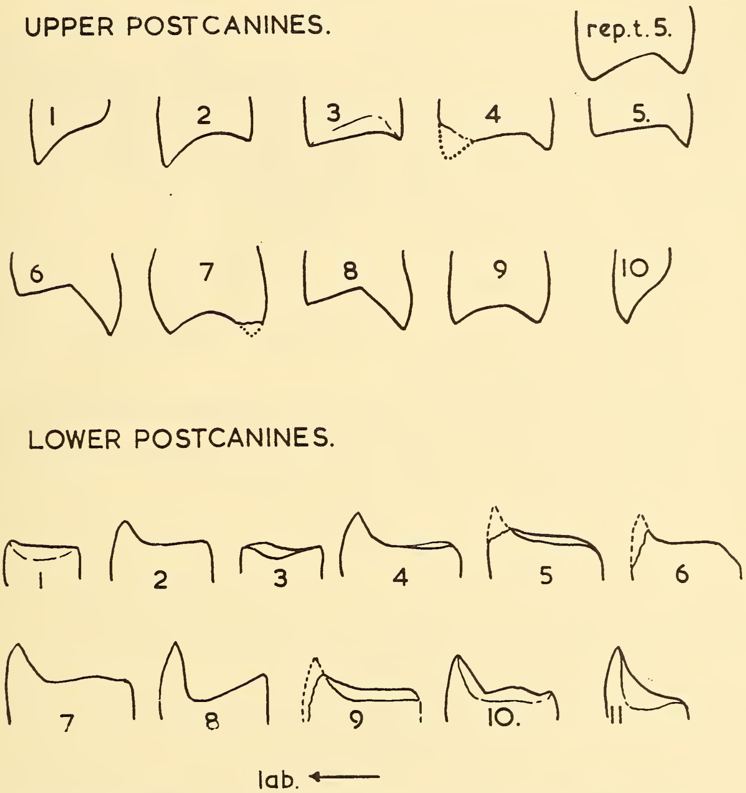

FIG. 8.—*Bauria cynops*. Posterior views of upper and lower postcanines. All × 3.

same level as the remaining lower incisors so that it can easily be mistaken for a lower incisor.

The postcanine series follow immediately after the canine without an intervening diastema. As in the case of the upper jaw the postcanines of both sides are arranged to form an arc, and the two arcs diverge away from one another in front and behind the 5th postcanine. Eleven postcanines are present on both sides. In crown view the postcanines are transversely ovate but have a greater eccentricity than the corresponding uppers.

The 10th left postcanine shows the least signs of wear (Plate XIV B; fig. 8). It consists of a prominent labial cusp. The remainder of the crown is flat except for a faint ridge along the lingual edge and a prominent medium transverse ridge. This ridge is drawn upwards to form an ill-defined cusp in the centre of the crown. Faint ridges extend from the apex of the main cusp along the anterior and posterior borders of the crown. On the right side the 10th post-canine is an old tooth which had not been replaced before death, and is greatly worn.

In the 9th left postcanine the main cusp has been lost, but the medium transverse ridge, although slightly worn, can still be recognized.

In the 4th, 5th and 7th postcanines initial wear stages are present. The central ridge has been worn away and a basin is present in the centre of the crown lingually to the main cusp. This basin is flanked in front and behind by the two ridges extending inwards from the apex of the main cusp. In the 8th tooth wear is further advanced and this basin has deepened considerably. Consequently the main cusp is more prominent in this tooth than in unworn teeth. In the 6th postcanine wear has advanced further. The main cusp is low and an oblique wear-facet is present on the lingual surface of the crown. The crowns of the 1st and 3rd teeth are smaller than adjacent teeth and are worn to a flat horizontal surface. The 11th postcanine is much smaller than the remaining postcanines; it consists of a prominent labial cusp lingually of which the crown falls rapidly away.

As in the upper postcanines, a small gap separates consecutive crowns. The gaps are larger anteriorly than posteriorly. The measurements of the individual postcanines, given in mm., are as follows:

	1	2	3	4	5	6	7	8	9	10	11
Max. ant.-post.	2·2	2·5	2·2	3·0	3·0	3·2	3·4	3·0	3·3	?	2·8
Max. ling.-lab.	3·2	4·2	3·4	4·8	4·8	4·8	5·4	4·8	5·1	4·2	3·5

Relationship between the wear pattern of upper and lower postcanines

An outstanding characteristic of the dentition is that in the initial wear stages the upper teeth are subject to wear mostly on their labial edge and centre of the crown, whereas in the lower postcanines wear is greater in the centre of the crown and on the lingual edge. It is only in very advanced wear stages that postcanines tend to acquire nearly flat occluding surfaces.

Although an attempt has been made to illustrate (fig. 10) the three progressive stages of wear of *Bauria* postcanines, it is naturally difficult to determine from one specimen the exact changes the postcanine teeth underwent as a result of wear. Careful investigation of other bauriamorph specimens will be necessary to confirm these findings. The initial wear (fig. 10 A, I) in the centre of the lower postcanines, and wearing away of the upper labial cusps, is apparently due to the upper labial cusp meeting the lower postcanine lingually of the lower labial cusp. The lingual edge of the upper tooth occludes lingually of the lingual edge of the lower teeth and this results in the formation of the oblique wear-facet extending upwards and inwards from the lingual edge of the upper postcanines. In a more advanced stage (II) an oblique wear-facet is developed on the lingual edge of the lower teeth where the oblique wear-facet of the uppers meets the lowers. Consequently both upper and lower are worn away on their lingual sides during this phase. In an advanced wear stage (III) all

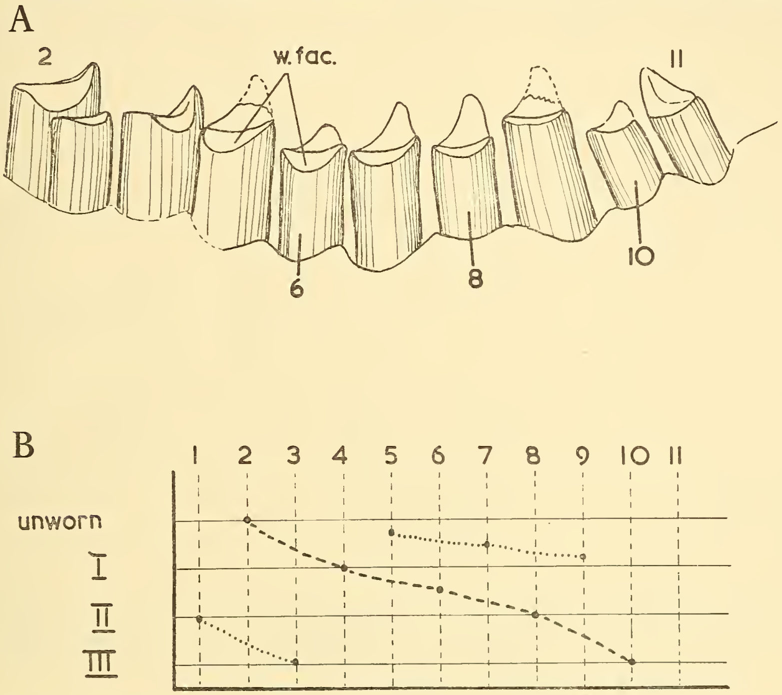

FIG. 9.—*Bauria cynops.* A, medial view of the right lower postcanine series and B, graph to illustrate decrease in extent of wear of odd and even-numbered postcanines. Wear stages I, II, and III correspond to those shown in Fig. 10. A × 3. (Key to lettering, p. 255.)

the prominent features of the crown tend to be worn away so that only flat occluding surfaces remain.

The height of the crown above the alveoli borders varies greatly in consecutive postcanines. As a general rule the height is greater in unworn teeth than in worn teeth. The result is that wear-facets of consecutive teeth are seldom on the same horizontal plane (fig. 9 A).

The correct interpretation of the degree of wear is of importance in determining the order of tooth replacement in the postcanine series.

Roots of postcanines and alveoli

Several teeth are loosely held in enlarged alveoli whereas others are tightly held by their alveoli. In the latter the alveoli are built up on the lingual side of the tooth in such a way that a horizontal shelf is formed at the base of the lingual side of the postcanines. This is more marked in the upper jaw than in the lower. As a general rule worn teeth are tightly held and unworn teeth loosely.

A fracture through the right ramus of the lower jaw has exposed the roots of the 6th and 7th postcanines (fig. 7 B, C). The single root of the 7th is substantial and tapers gradually to a point. There is no indication of any division of the root. The alveolar bone is closely apposed to the root. A narrow

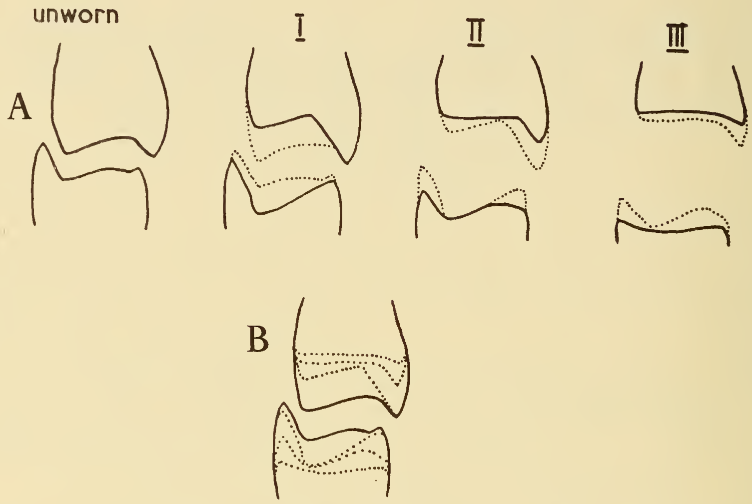

Fig. 10.—*Bauria cynops*. A, occlusal relations of unworn and three wear stages typical postcanine teeth and B, three wear stages compared with unworn upper and lower postcanines. All × 3.

bony transverse septum separates successive teeth. The remnants of the septum between the 6th and 7th obscure part of the root of the 6th postcanine. Preservation of the dentary surrounding the root is not exceptional, but it is possible to recognize large cavities and canals lingually to the apex of the root. In addition the root is slightly resorbed on its lingual side.

Unfortunately no sections through the root of an upper postcanine exist. Reconstructed sections based on external features only are given in fig. 6 A, B, C. Features that could not be observed are shown in dotted lines. Posterior to the secondary palate a thick mass of bony tissue constituted by the maxilla and a thin plate of the palatine (PAL) lies lingually to the last six teeth (fig. 6 C). The medio-ventral edge of this bony mass is drawn downwards to form a prominent ridge so that a narrow groove separates the outer surface of this ridge from the teeth. A longitudinal section was cut through the bony mass. Numerous cavities and canals are present in it, but their shape and course could only be accurately determined if serial sections were made. Anteriorly this lingual mass of bone is obscured by the presence of secondary palate, but the ridge on the lingual edge of the lingual mass continues forward close to the lingual surface of the teeth.

Tooth replacement

Only in one case are a functional tooth and its successor preserved and visible in a single alveolus. This supplies important information on how tooth replacement actually takes place, and details on the structure of an unworn crown.

The tooth preserved in the act of replacing is the 5th right upper (fig. 6 B). Its alveolus is greatly enlarged. The functional tooth lies hard against its labial edge. The crown of a replacing tooth is situated lingually and slightly behind the functional tooth. The lingual edge of the replacing tooth is preserved at the same level as the edge of the alveolus. The replacement tooth is obliquely orientated and does not, as would be expected, erupt vertically downwards, but rather downwards and inwards. The lingual edge of the root of the functional tooth has been resorbed and the labial edge of the replacing tooth is closely apposed to it. After the functional tooth was lost, the crown of the replacing tooth would presumably have moved in a labial direction to the vertical position. On the left side replacement was in advance of that on the right because the old functional tooth has been shed and an unworn replacement tooth is present. Although the alveolus is still greatly enlarged the new tooth is vertically orientated. Alveoli size is therefore important in determining the order of tooth replacement. Although horizontal sections through the bony mass lingual to the last 7 upper postcanines revealed no additional replacing teeth, the wear patterns of adjacent teeth appear to indicate that active replacement of the postcanines was probably still taking place in both upper and lower jaws although in no case in the lower jaw are both the replacing and old functional teeth preserved in a single alveolus. A probable explanation for this is that the replacing teeth developed initially deep in the maxilla or dentary lingually to the apex of the roots of the functional teeth. An empty cavity in this position alongside the root of the greatly worn 6th lower postcanine appears to confirm this view. Replacing teeth would therefore only become visible lingually to the functional teeth shortly before eruption. It was considered inadvisable to section the type to confirm this view. Boonstra (1938) mentioned a series of replacing teeth lingual to the functional postcanines exposed by grinding in the American Museum specimen, but did not give a detailed description.

In *Ericiolacerta* the replacing teeth are visible throughout their development, and the order of replacement is easily determined. In the present specimen of *Bauria* the order of replacement has to be determined by other criteria such as the degree of wear of the postcanines, size of alveoli, and size of individual teeth. These alone are insufficient because, for example, if replacement in both jaws is not accurately synchronized, occluding teeth of different ages may well produce different wear patterns in teeth of similar age.

It seems clear from the presence of unworn teeth in the postcanine series and the actual replacement observed, that tooth replacement is still taking place throughout the postcanine series. The available evidence suggests that teeth replace alternately in *Bauria* as in *Ericiolacerta*. For example, in *Bauria*, in the right mandible (fig. 9 A), the 6th, 8th and 10th postcanines are slightly smaller, are more tightly held by their alveoli, and are lower in height above the alveolar border than the 5th, 7th or 9th. Wear is certainly further advanced in the former group. Similar conditions can be observed in the left mandible. The 9th, 7th and 5th postcanines are larger, more loosely held in their alveoli, and higher than the 6th and 8th. In the left mandible, replacement is in advance of that of the right.

In the left maxilla the 5th and 7th are large, unworn, loosely held in their alveoli, and high-crowned in contrast to the 6th and 8th.

Replacement in the right maxilla also lagged slightly behind that in the left, and the replacing tooth for the 5th had not yet erupted before death. Alternate teeth throughout the series did not erupt simultaneously. For example, the right 7th upper postcanine already showed signs of wear although the 5th had not yet erupted. On the left the 5th alveolus is larger than the 7th. The 10th postcanine in the left mandible had been replaced only shortly before death, yet the 8th is well worn and in life would presumably have been the next to be replaced. This evidence suggests that a wave of replacement moved forwards along the odd- and even-numbered postcanines. In the case of the maxilla, the wave that affected the odd-numbered postcanines was in advance of that which affected the even-numbered, but the waves are spaced so that alternate replacement is present over short distances.

An expected result of replacement waves moving in an anterior direction would be that the wear of alternate teeth would diminish in an anterior direction. There is some evidence of this (fig. 9 B). In the right mandible the 10th postcanine is greatly worn and was about to be replaced. The 8th and 6th teeth are well worn but the 4th is less worn. The 2nd tooth appears to have erupted shortly before death and shows few signs of wear. The 9th, 7th and 5th, on the other hand, appear also to have erupted shortly before death and are not much worn, whereas the 3rd is small, greatly worn and loosely held in its alveolus, and presumably would have been the next to be replaced. The three wear stages upon which fig. 9 B is based correspond to those shown in fig. 10. Similar facts were observed in the maxilla.

Tooth replacement in occluding upper and lower jaws appears to have been fairly closely correlated, with the result that a recently erupted and unworn tooth of the upper jaw would have met a recently erupted and unworn tooth of the lower jaw. For example, in both upper and lower jaws on the right side the 9th, 7th and 5th postcanines appear to have been replaced shortly before death.

Discussion

In both *Ericiolacerta* and *Scaloposaurus* there was a marked reduction in the size of the canines. The postcanine teeth of both genera are similar. Both are circular in cross-section at the alveolar border and in both there is a tendency to develop small cusps although these are limited to the lower jaw in *Ericiolacerta*. In *Scaloposaurus* the shearing action of the postcanine teeth has been retained, but in *Ericiolacerta* the reduction of the canines has apparently made it possible for the apices of the upper and lower postcanines to meet despite the limited area of contact, and the apices of the crowns are completely worn away in old teeth.

It is not possible to determine whether the shearing action was retained in *Ericiolacerta* or whether a limited amount of lateral and propalinal jaw movement was possible. One of these three movements may account for the wear-facets on the postcanines of *Ericiolacerta* which could not be accounted for only by a simple dorso-ventral movement of the lower jaws relative to the uppers.

In *Bauria* and all bauriamorphs from the *Cynognathus* zone the teeth have expanded transversely to increase the occlusal areas. The crushing action of *Bauria* is therefore much more efficient than that of *Ericiolacerta*, and the latter appears to be very close to ancestral forms which deviated away from a simple sectorial action of apposing dentitions.

A similar shift from a sectorial dentition to a crushing dentition took place in some early mammals (Patterson, 1956), e.g. the dryolestids. Here, too, there has been a reduction in the size of the canines. The development in the bauriamorphs paralleled that of some of the later mammals and consequently there is no question of the known bauriamorphs being ancestral to any known Jurassic or Rhaetic mammal. A possible exception is *Diarthrognathus*. This form may have developed from early bauriamorphs, and because it possesses a squamoso-dentary articulation may therefore be classified as a mammal.

The late cynodonts also developed a crushing dentition, but a reduction of the size of the canines does not appear to have triggered off this development. In cynodonts such as *Diademodon* the sectorial action was retained and a crushing part of the tooth added lingually to the original labial shearing cusps, the apices of which never met.

It has been tacitly assumed that the flat crowns of *Bauria* are the result of a grinding action of the jaws. Because of the mode of replacement in *Bauria* the crowns of the postcanine teeth are of varying heights. Consequently, for individual teeth of the upper and lower jaws to have met it is necessary for the teeth to intermesh. This would appear to have ruled out any significant propalinal movement of the mandible. The large upper canine, the pit for the lower canine, the large lingual cusps of the lower postcanines, and the transverse processes of the pterygoid would probably eliminate any significant lateral movement of the mandible. For this reason it is unlikely that true grinding was developed in *Bauria* but that the upper and lower teeth could only crush food as the result of a simple pounding action. Unfortunately details of the nature of the mandibular joint in *Bauria* are not available. Recent work to be published shortly on the jaw action of gomphodont cynodonts has indicated that it is unlikely that any propalinal movement was present in these forms and that the wear pattern of the postcanines which suggest propalinal movement are due to other factors.

In *Ericiolacerta* and *Bauria* it has been shown that the teeth replaced alternately. There is no question, therefore, that a mammalian type of dental succession was present in either of these bauriamorphs. In *Ericiolacerta* it has been shown that the replacing teeth developed initially in distinct pits in the dentigerous bones and lie lingually to the functional dentition. The pits were connected by a shallow longitudinal groove, which presumably housed the dental lamina. As the replacing teeth increased in size their pits enlarged and became confluent with the alveoli of the functional teeth, and the replacing teeth moved labiad. Recent work to be published in the near future has shown that in the *Cistecephalus* zone cynodonts, in *Thrinaxodon* and in *Tribolodon*, the replacement teeth developed in a similar fashion. This type of replacement was not confined to mammal-like reptiles. In his excellent résumé on tooth replacement Edmund (1960) has cited the relevant literature and has pointed out that in *Nothosaurus* and *Pleisiosaurus* replacing teeth developed in an almost identical fashion to that described above. Edmund (1957) has shown that in ornithischian dinosaurs a groove for the dental lamina connected a series of foramina which penetrated the dentigerous bone and opened into the alveoli of the functional teeth. Tooth germs budded off from the dental lamina and passed through these foramina into the base of the alveoli.

In *Bauria* the teeth did not develop in superficial pits, but apparently deep in the dentigerous bones lingually to the base of the roots of the functional teeth. No indication of a groove for the dental lamina or any foramina (gubernacular canals) which connected the developing teeth with the oral epithelium could be observed, but better material is necessary to confirm this point. This may be interpreted to mean that tooth replacement has ceased in the particular specimen of *Bauria* described above, but this is unlikely. To obtain the type of replacement found in *Bauria* and in mammals it was necessary for the dental lamina or remnants of it to lie not superficially but to be buried within the dentigerous bones. A similar development has taken place in the crocodiles (Edmund, 1960), where remnants of the dental lamina remain in each alveolus and retain their capacity to form teeth. The reason for the shift in *Bauria* to a deep site for the development of the replacing teeth was presumably correlated with the transverse widening of the teeth in this form. If the developing teeth were to have developed in superficial pits they would have projected into the oral cavity and either been damaged by or hindered mastication. A similar shift from a superficial to deep-lying position took place in other groups which have transversely widened teeth, e.g. *Diadectes*, Watson (1954). In *Diademodon* replacing teeth also developed deep in the dentigerous bones below the functional teeth, but the groove for the dental lamina remained in the superficial position lingually to the bases of the postcanines. A similar shift from a superficial site for replacing teeth to a site deep in the dentigerous bones probably took place in the ancestors of mammals. In mammals, in contrast to

Bauria and *Diademodon*, developing permanent teeth retain their contact with the oral epithelium through their gubernacular canals.

The origin of the mammalian dental succession from the types of dental succession reported in mammal-like reptiles remains an unsolved problem. *Bauria* shows that alternate replacement was present in advanced mammal-like reptiles and that teeth did replace alternately even though expanded transversely. It is pertinent to mention that alternate replacement was also still present in the advanced mammal-like reptile (or early mammal) *Diarthrognathus* from the late Trias. This does not support the view of Bolk (1922) that as the postcanines became more complex they would no longer erupt alternately but that one of the alternate-numbered series would actually replace the other series, one becoming the deciduous and the other the permanent. The specialized conditions in gomphodont cynodonts do not help to solve the problem of the origin of the mammalian succession. An alternate explanation for the mammalian dental succession has been suggested by Edmund (1960). Edmund has shown that in early tetrapods such as *Captorhinus* the teeth of a single *zahnreihe* erupt as a unit and are ankylosed to the dentigerous bones. Edmund has suggested that in mammals the deciduous teeth represent the remnants of one *zahnreihe* and permanent dentition a second anterior *zahnreihe*. This theory also explains the front-to-back order of replacement in mammals and, because of its simplicity, is extremely attractive. But certain problems present themselves. Edmund made no attempt to correlate his theory with palaeontological evidence. Eruption and functioning of teeth in a complete *zahnreihe* is known only in a few specialized groups such as the captorhinids. In mammal-like reptiles alternate tooth replacement similar to that of typical reptiles is present except in the specialized gomphodont cynodonts, where the position is difficult to ascertain.

Edmund's theory would imply that in the late mammal-like reptiles there should be a tendency to reduce the number of teeth to two *zahnreihen*, but no tendency in this direction has been reported.

Although these facts alone do not disprove Edmund's view they certainly do not confirm it. An alternative explanation for the origin of the mammalian conditions is worth while considering. It is possible to derive the mammalian succession from forms in which the time lag between the budding-off of the even- and odd-numbered tooth germs from the dental lamina is reduced so that odd- and even-numbered teeth can erupt consecutively and function simultaneously. Even in mammals consecutive teeth in the series do not erupt one after the other in an orderly fashion; e.g. in man the first deciduous molar erupts before the deciduous canine, and the first molar erupts before the second premolar. Compared with the pelycosaurs there appears to be a tendency to reduce the relative time-interval between the eruption of alternate teeth in later mammal-like reptiles. In pelycosaurs there is a tendency for the odd- and even-numbered teeth not to function simultaneously. This has been termed 'functional distichial replacement' by Kermack (1956). He has pointed out that functional distichial replacement is not present in the therocephalians and gorgonopsians studied by him. On the other hand, although alternate tooth replacement is present in *Thrinaxodon* and *Bauria*, the functional periods of odd- and even-numbered teeth overlap considerably. A reduction of the time-lag between the formation of odd and even teeth together with a lengthening of the time between eruption and replacement of individual teeth would be expected if the form were moving towards the mammalian type of replacement. It is difficult because of lack of reliable evidence on tooth replacement in mammal-like reptiles to determine a trend of this nature, but tooth replacement was apparently far less frequent in a form such as *Bauria* than in *Ericiolacerta*. A similar reduction of the frequency of replacement can be traced in the later cynodonts compared with those of the *Cistecephalus* and *Lystrosaurus* zones. What is urgently required is further growth series of individual mammal-like reptiles.

Summary

(1) The dentition, tooth replacement and wear stages of the postcanine teeth of the type specimens of *Ericiolacerta parva* and *Bauria cynops* are described.

(2) In both genera alternate tooth replacement was present. In *Ericiolacerta* the replacing teeth developed initially in pits in the base of the superficial groove which supported the dental lamina. In *Bauria* replacing teeth appear to have developed deep in the dentigerous bones. The origin of the mammalian order of replacement is briefly discussed.

(3) *Ericiolacerta* represents an early stage in the transition from a sectorial to a pounding or crushing dentition. This transition was probably correlated with reduction of size of the canines in this form. In *Bauria* a crushing dentition is better developed than in *Ericiolacerta*.

(4) It is doubted whether a true grinding action was present in *Bauria*. Wear of the postcanines could be accounted for solely by a simple pounding action.

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Key to Lettering

at. bo.	Attachment bone.
c.	Canine.
can.	Canal in dentary.
DEN.	Dentary.
f. t. 5	Functional 5th postcanine.
lab.	Labial.
lab. c.	Labial cusp.
l. c. p.	Pit for lower canine.
ling.	Lingual.
long. gr.	Longitudinal groove.
MAX.	Maxilla.
p.	Pit for replacing tooth.
PAL.	Palatine.
p. for.	Palatal foramen.
rem. f. 11	Remnant of 11th functional tooth.
rep. t.	Replacing tooth.
rep. t. 11	11th replacing tooth.
sec. p.	Secondary palate.
V.	Vomer.
w. fac.	Wear-facet.
w. fac. h.	Horizontal wear-facet.
w. fac. o.	Oblique wear-facet.